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PRODUCTION AND DECOMPOSITION OF THE ROOTS AND RHIZOMES OF SEAGRASSES, *ZOSTERA MARINA* AND *THALASSIA TESTUDINUM*, IN TEMPERATE AND SUBTROPICAL MARINE ECOSYSTEMS

W. Judson Kenworthy and Gordon W. Thayer

ABSTRACT

Seagrasses, *Zostera marina* in temperate regions and *Thalassia testudinum* in subtropical and tropical areas, form the basis of highly productive subtidal wetlands. We present our research results and a review of the literature concerning production, biomass and decomposition of roots and rhizomes of these seagrass species. *Zostera* rhizomes and roots are a substantial source of organic matter to estuarine sediments. During early stages of decay the roots and rhizomes leach soluble organic matter that is readily utilized by bacteria. The remaining particulate fraction decomposes slowly and has a larger pool of refractory material than the leaves. Thus, the particulate fraction of *Zostera* roots and rhizomes provides a large and relatively enduring source of organic detritus, which is available even during periodic fluctuations in above-ground production by this seagrass and other autotrophs. Under ambient conditions *Thalassia* rhizome decay was significantly slower than that for *Zostera*, while root decay rates were similar. The turnover rates for these two seagrasses suggest differences in the potential sources and availability of nutrients in sediments of temperate and tropical seagrass meadows. The contribution of seagrass root and rhizome detritus to the energetics and nutrient cycles of benthic ecosystems is discussed.

Seagrasses are common in shallow marine waters throughout temperate and tropical regions of the world (den Hartog, 1970; McRoy and Helfferich, 1977; Phillips and McRoy, 1980). Except for the genus *Phyllospadix*, all seagrasses require an unconsolidated substratum to which they are secured by roots and rhizomes (den Hartog, 1970). Unlike the typical holdfast of most macroalgae, the roots and rhizomes of seagrasses penetrate the substrate, depositing organic matter directly into the sediment (Fig. 1).

Because a large portion of marine vascular plant production is not consumed directly by herbivores (Teal, 1962; Mann, 1972; Ogden, 1980), many investigations have focused on the formation and utilization of organic detritus originating from the plant material. The main research emphasis on seagrass decomposition has been on the leaves, especially the process of particulate decay (Zieman, 1968; Fenchel, 1970; Harrison and Mann, 1975; Josselyn and Mathieson, 1980; Robertson et al., 1982; Thayer et al., in press), leaching of dissolved organic matter (Godshalk and Wetzel, 1978; Robertson et al., 1982), and aspects of biochemical composition and utilization of the detrital particles (Tenore, 1975; 1981; Harrison, 1977; Tenore et al., 1977; Hanson, 1982; Robertson et al., 1982).

Even though the physical, chemical and biological aspects of the sediments of seagrass meadows have drawn considerable attention (Wood et al., 1969; Scoffin, 1980; Burrell and Schubel, 1977; Fonseca et al., 1982; Kenworthy et al., 1982; Short, 1983), little data are available on the production and utilization of organic matter originating from seagrass roots and rhizomes. Estimates of below-ground biomass for many seagrasses suggest that the roots and rhizomes of these plants contribute a substantial amount of organic matter to the sediments (Zieman, 1982; Thayer et al., in press).

Seagrass meadows are the location for extensive nutrient cycling processes

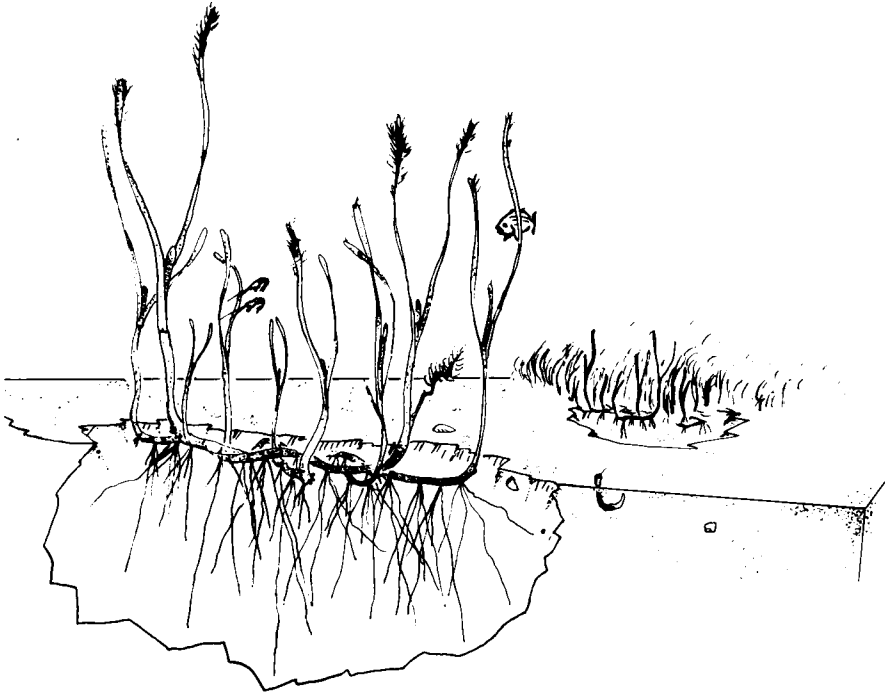


Figure 1. Illustration of a *Zostera marina* meadow showing the below-ground roots and rhizomes.

(McRoy and Barsdate, 1970; Kenworthy et al., 1982; Iizumi et al., 1982; Short, 1983), high primary production (Zieman and Wetzel, 1980), and relatively large concentrations of plant and animal biomass (Thayer et al., 1975; Kikuchi and Peres, 1977). Large amounts of organic matter are required to sustain the essential processes and functions of the seagrass ecosystems. Part of the requirements for benthic heterotrophic processes, and indirectly for the epibenthos, may be met by the decomposition of organic matter derived from roots and rhizomes. The roots and rhizomes are produced in place, deposited unaltered and very little is transported from the meadow.

In this paper we present the results of our research and review the literature in order to develop hypotheses on the functional role of the organic matter derived from the production of the roots and rhizomes of seagrasses.

METHODS AND MATERIALS

Study Sites.—This study was conducted at two sites. The first site, Back Sound, is a warm, temperate seagrass ecosystem in a coastal plain estuary (Pritchard, 1967) located at approximately lat. 35°41'N, long. 76°37'W near Beaufort, North Carolina, U.S.A. Back Sound is vegetated by two seagrasses, *Zostera marina* and *Halodule wrightii* (Kenworthy, 1981). The second site, Cross Bank in Florida Bay, is a subtropical marine estuary located in southern Florida, U.S.A., at approximately lat. 25°00'N, long. 80°35'W. Florida Bay is typical of many subtropical and tropical seagrass ecosystems in the western hemisphere and has three principal species that cover approximately 70–80% of the bay bottom, *Thalassia testudinum*, *Syringodium filiforme* and *Halodule wrightii* (Zieman, 1982). Although a mosaic of species distribution and abundance occurs throughout the Bay, *T. testudinum* is the dominant species.

Plant Biomass.—The biomass of seagrasses was estimated from samples (no less than triplicate) taken with a 15 cm diameter corer inserted to a depth of 25 cm into the sediment. The entire plug of seagrass and sediment was removed, and the plant material was washed free of sediments and separated into either leaves or combined roots and rhizomes for *Z. marina* and *H. wrightii* and into leaves, short shoot sheaths, living rhizomes, decaying rhizomes, living roots and decaying roots for *T. testudinum*.

The sorted plant material was rinsed in a solution of 10% HCl to remove encrusting carbonate epiphytes. All plant components were dried to a constant weight by lyophilization and weighed to the nearest 0.001 g. Ash free dry weight of plant material was determined after combustion at 500°C for 24 h. Additional estimates of plant biomass which had been determined by reasonably comparable techniques were taken from the literature (Patriquin, 1973; Riner, 1976; Sand-Jensen, 1975; Jacobs, 1979; Zieman, 1982).

Seagrass Production.—*Zostera* production was estimated by a recently developed leaf marking technique (D. G. Patriquin, unpubl. data, Dalhousie University, Halifax, Nova Scotia; Jacobs, 1979; Kenworthy, 1981) that incorporated dimensional analysis of leaf, root and rhizome components of the plant. This technique enables in situ net production of leaves, roots and rhizomes to be estimated simultaneously. Estimates of *Thalassia* production were calculated from the literature (Patriquin, 1973; Bittaker and Iverson, 1976; Zieman and Wetzel, 1980).

Decomposition of Particulate Organic Matter in Litter Bags.—Live roots and rhizomes of *Z. marina* and *T. testudinum* were collected from established meadows at each study site, washed free of sediment, sorted and weighed wet (nearest 0.001 g). Approximately 10 g of each material were placed in 2.0 mm mesh litter bags made of fiberglass window screen. Subsamples of fresh material were removed to establish wet to dry weight conversions, initial ash free dry weights, carbon and nitrogen content and fiber analysis (Goering and Van Soest, 1970). Carbon and nitrogen were determined by a Carlo Erba Model 1106 elemental analyzer standardized with orchard leaves (National Bureau of Standards Reference Material).¹

Zostera litter bags were buried in the sediment to a depth of 3–5 cm in two seagrass habitats near Beaufort, North Carolina, representative of: (1) an open-water shoal consisting of a coarse sand substrate with relatively lower concentrations of organic matter, total nitrogen and nitrogen cycle intermediates, dissolved ammonium and exchangeable nitrogen and (2) a protected embayment having a silty substrate and measurably greater amounts of organic matter, total nitrogen and nitrogen cycle intermediates (Kenworthy et al., 1982). These environmental conditions offered us an opportunity to compare decomposition in nutrient-rich and relatively nutrient-depleted sediments. During 170 days from April to September 1981, litter bags were retrieved periodically and washed free of sediment. After the contents of the bags had been dried to a constant weight by lyophilization ash-free dry weight and carbon and nitrogen analyses were determined on subsamples.

Thalassia testudinum litter bags were buried at a depth of 5–10 cm in the sediment on Cross Bank. Our selection of burial depths for both *Zostera* and *Thalassia* was based on observations of the maximum dead root and rhizome mass in undisturbed seagrass meadows. Cross Bank is typical of *Thalassia* habitats located on the numerous carbonate mud banks (shoals) occurring throughout Florida Bay. Due to sedimentation and periodic exposure at these locations the plants frequently suffer high mortality, causing the formation of large quantities of root and rhizome detritus that is incorporated in the sediment. Periodically during 247 days from December 1982 to August 1983, the litter bags were recovered and processed in the same way as for the *Zostera* samples.

Production and Utilization of Dissolved Organic Carbon (DOC).—*Zostera* plants were collected in the vicinity of Beaufort, rinsed free of sediment and sorted into either leaves or roots-rhizomes, which were treated separately throughout this experiment. To account for possible physico-chemical differences resulting from different-aged plant material, only the third oldest leaf on a shoot and only the most recently produced roots and rhizomes were used. Ten subsamples of each type of material were separated, weighed wet and dried to a constant weight by lyophilization to establish a wet to dry weight conversion factor. The plant material was sterilized by exposure to approximately 2.4 Mrads of gamma radiation from a Co-60 source at the Oak Ridge National Laboratory (Mills and Alexander, 1976).

Five flasks, each containing 200 ml of filtered (0.2 μ m) offshore seawater, were autoclaved. Approximately 200–250 mg of irradiated plant material were transferred by sterile technique into each flask under a laminar flow hood. Two flasks of leaf, two flasks of root-rhizome and one flask without plant material were incubated in the dark at 20°C for 70.5 h and gently aerated with filtered, sterilized air.

At 0.0, 4.5, 23.0, 28.0 and 70.5 h, a sterile technique was used to withdraw two 5 ml samples from each flask. To verify that the contents were sterile, bacteria were enumerated from a subsample of each 5 ml by the acridine orange direct count method (AODC) (Hobbie et al., 1977). Another subsample

¹ Reference to trade name does not imply endorsement by the National Marine Fisheries Service, NOAA.

of each of the 5-ml samples was used for DOC analysis. The liquid was filtered through a 0.2 μm nuclepore membrane and DOC was measured on an Oceanography International Carbon Analyzer following potassium persulfate wet oxidation of the DOC to CO_2 (Menzel and Vaccaro, 1964).

After the DOC had been leached, the sterile liquids with DOC originating from the leaves were pooled separately as were the root-rhizome liquids. Each liquid fraction was passed through a 0.2 μm nuclepore membrane to remove any particulate organic matter. Flasks containing 150 ml of liquid with leaf DOC, root-rhizome DOC and with filtered, autoclaved seawater were prepared. Thus, three treatments were assessed: leaf DOC, root-rhizome DOC and a control without any plant DOC.

Environmental conditions for the utilization phase of the experiment were identical to the leaching experiment. The utilization experiment was initiated by adding 1 ml of inoculum from a flow-through seawater system that contained decomposing seagrass. The inoculum was pre-filtered through a 1.0 μm filter to exclude larger heterotrophs. At 0, 4, 7, 11, 24, 29, 36 and 40 h, each flask was sampled and analyzed in the same manner as described for the leaching experiments.

RESULTS

Biomass and Production.—Biomass of the living roots and rhizomes of *Z. marina* in North Carolina ranged between 45 and 285 $\text{gdw} \cdot \text{m}^{-2}$ and was in the range of other reported values (Table 1). A seasonal trend was apparent with the largest biomass occurring in spring and early summer and declining in late summer (Fig. 2A). A regrowth period was evident between October and January. In North Carolina, *H. wrightii* contributed additional below-ground biomass throughout the year, exceeding that of eelgrass during late summer. Approximately 90% of the biomass was located in the upper 10 cm of the sediment profile. Rhizome biomass in an eelgrass bed in New York ranged between 660 and 950 $\text{gdw} \cdot \text{m}^{-2}$ (Table 1; Fig. 2B) and also exhibited a recognizable seasonal maximum and minimum (Riner, 1976).

Root, rhizome and leaf biomass for *T. testudinum* generally was greater than for eelgrass (Table 1). Since the rhizome of *T. testudinum* may be buried to depths exceeding 10 cm, biomass of the non-photosynthetic portion of the short shoot, the sheath, also is deposited directly into the sediment. The proportion of detrital organic matter originating from below-ground biomass of both species was large (Table 1; Fig. 2B).

Most of the below-ground eelgrass production was by the rhizome (Kenworthy, 1981). Production for roots and rhizomes of eelgrass ranged between 55 and 182 $\text{g C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ (Table 1). The range for *Zostera* in North Carolina, 55–102, is representative of averages for low and high plant densities, respectively. The lower value illustrates a situation where plant density was dramatically reduced during summer, and the higher value a situation where higher shoot densities were maintained for a longer period during the plants' annual cycle. Estimates for *Thalassia* root and rhizome production were similar to those for *Zostera* (Table 1). For both species, leaf production generally exceeded production of roots and rhizomes.

Plant Composition.—The roots and rhizomes of both *Zostera* and *Thalassia* had a larger proportion of structural carbohydrates than the leaves (Table 2). The largest fraction of the structural carbohydrates of roots and rhizomes of both species consisted of cellulose and hemicellulose. *Zostera* leaves had a higher proportion of total nitrogen and a C:N ratio of 21, much lower than the ratios 43 and 65 for either roots or rhizomes, respectively. The nitrogen content of the roots and rhizomes of *Thalassia*, although generally higher than for the roots and rhizomes of *Zostera*, was considerably lower than that for leaves of either species.

Litter Bag Decomposition.—*ZOSTERA MARINA*. During the 170-day decomposition period, approximately 50–60% of the organic matter in the rhizome bags and 40–

Table 1. Representative values for the ranges and averages of below-ground biomass, net productivity and standing crop of *Zostera marina* and *Thalassia testudinum*

Species	Location	Plant component	Productivity annual g C·m ⁻² ·yr	Living biomass g dw·m ⁻²	Detrital biomass
<i>Z. marina</i> ^a	North Carolina	Roots and rhizomes	55–102	45–285	—
<i>Z. marina</i> ^b	France	Rhizomes	182	49–244	100–253
<i>Z. marina</i> ^c	Denmark	Rhizomes	165	99–217	159–240
<i>Z. marina</i> ^d	New York	Rhizomes	—	660–950	960–1,360
<i>T. testudinum</i> ^e	Bermuda	Rhizomes	219	—	—
<i>T. testudinum</i> ^f	Northwest Florida	Roots and rhizomes	132	—	—
<i>T. testudinum</i> ^g	Florida Keys	Roots and rhizomes	—	321–2,346	—
<i>T. testudinum</i> ^h	Florida Bay	Rhizomes	—	383–479	89–219
		Roots	—	174–532	70–80
		Short-shoot sheath (non photosynthetic)	—	489–1,048	—
<i>Z. marina</i> ^{a,b,c,d}	North America and Europe	Leaves	300–400	50–200	—
<i>T. testudinum</i> ^f	Florida	Leaves	329–3,000	10–1,800	—

^a This study; ^b Jacobs (1979); ^c Sand-Jensen (1975); ^d Riner (1976); ^e Patriquin (1973); ^f Bitlaker and Iverson (1976); ^g Zieman (1982).

Table 2. Aspects of the composition of the leaves, roots and rhizomes of two seagrasses, *Zostera marina* and *Thalassia testudinum*. (All results represent the average of ≥ 3 determinations)

Source	Component (% of ash free dry weight)						
	Soluble (non-structural) carbohydrates	Cell wall constituents (structural) carbohydrates	Cellulose	Hemicellulose	Lignin	Silica	N
<i>Zostera</i> rhizome	46.9	53.0	18.3	28.9	3.5	1.8	0.66
<i>Zostera</i> roots	28.9	71.0	21.3	40.9	5.7	3.0	0.92
<i>Thalassia</i> rhizome	45.1	54.8	20.2	21.1	6.8	0.2	1.25
<i>Thalassia</i> roots	41.7	58.2	23.5	28.7	5.7	0.2	1.39
<i>Zostera</i> leaves	68.2	31.8	12.2	13.8	4.3	1.5	2.02
<i>Thalassia</i> leaves							
N = 3 ^a	65.1 ^a	34.9 ^a	—	—	—	—	—
N = 6 ^b	59.4 ^b	40.6 ^b	17.5 ^b	19.1 ^b	9.1 ^b	0 ^b	2.0 ^c
							42 ^c
							21 ^c

^a Robertson (1982); ^b Vincente et al. (1980); and ^c this study.

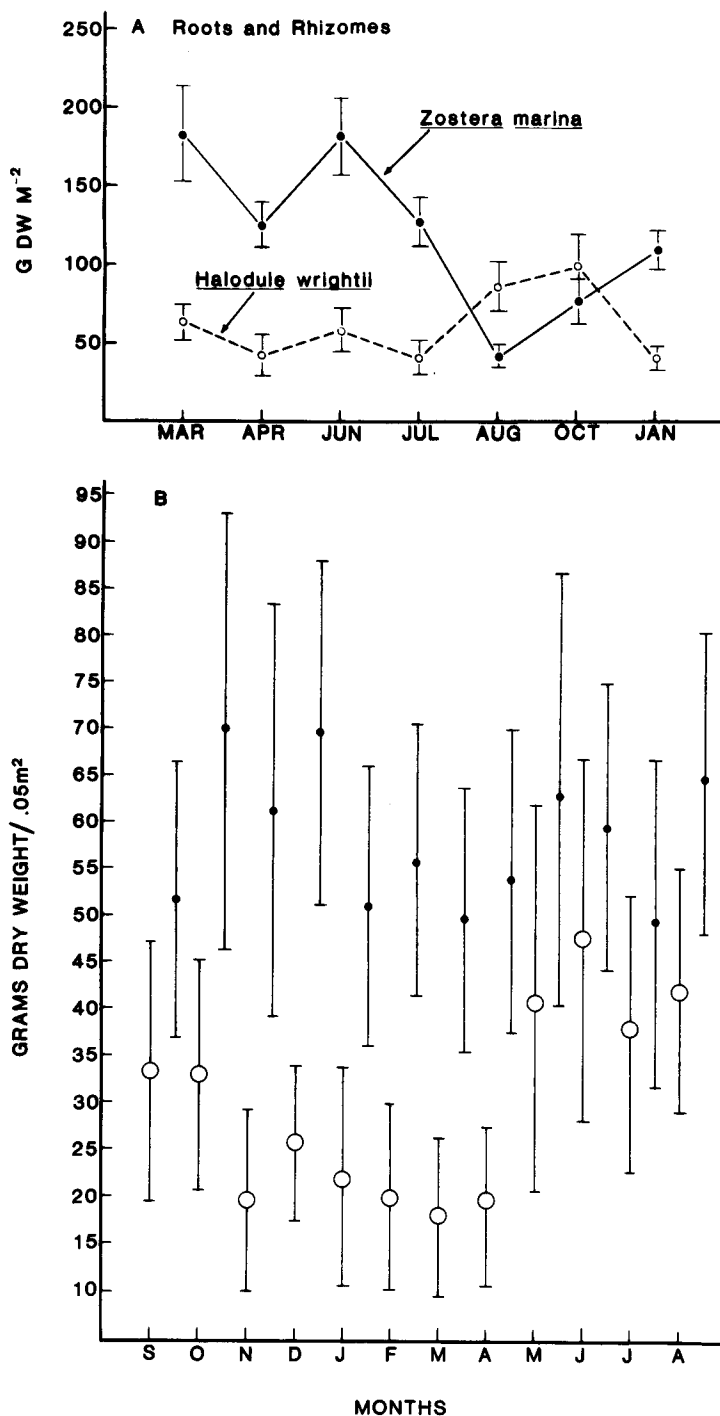


Figure 2. A. Seasonal cycle of below ground biomass in a seagrass *Zostera marina* and *Halodule wrightii* meadow in North Carolina. B. Seasonal cycle of the below ground biomass of living, O, and detrital, ●, rhizomes in a *Z. marina* bed in Long Island, New York. Data are from Riner (1976).

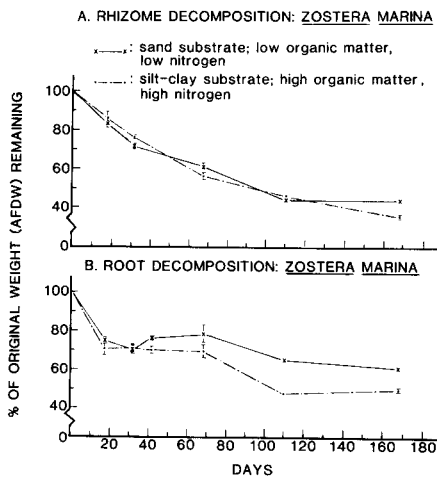
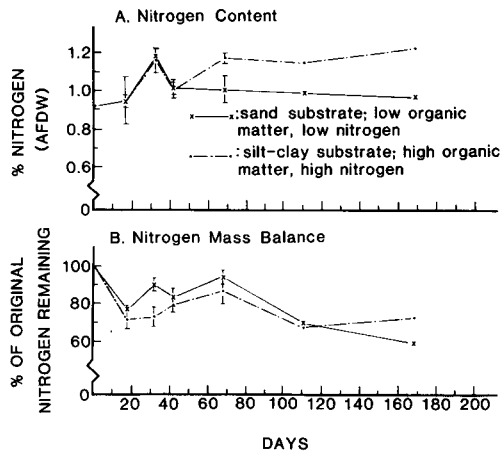
ROOT DECOMPOSITION: *ZOSTERA MARINA*

Figure 3. (Left) Weight loss (ash free dry weight) of *Zostera marina* rhizomes (A) and roots (B) placed in litter bags and buried in a *Z. marina* bed in North Carolina between April 1981 and September 1981. See figure for legend. Bars indicate ± 1 SE.

Figure 4. (Right) Changes in the nitrogen content (A) and mass of nitrogen (B) for *Zostera marina* roots in litter bags buried in a scagrass bed in North Carolina between April 1981 and September 1981. See figure for legend. Bars indicate ± 1 SE.

50% in the root bags were lost (Fig. 3). The rhizome decay rate declined with time and did not differ between sediment types. Roots decayed rapidly during the first 17 days, very little from day 18 to day 50, and slowly thereafter. During the first 70 days there were no major differences between the sediment treatments. Toward the latter part of the study, weight loss tended to be fastest in the root bags incubated in the sediment with the highest organic matter and nitrogen content.

There were small, but measurable, increases in percent nitrogen and a small decline in percent carbon over the course of the incubation in both the root and rhizome bags (Figs. 4–6). There were also small differences between sediment treatments that appeared toward the latter part of the incubation. The most demonstrable differences between sediment treatments occurred in the root incubations (Fig. 4).

Changes in nutrient composition resulted in approximately a 30% reduction in the C:N ratio for roots (initial C:N = 43:1, final C:N = 28:1) and rhizomes (initial C:N = 66:1, final C:N = 43:1). Although the percentage of nitrogen increased during the 170 days, a mass balance accounting showed a net decline in the absolute amount of nitrogen in the litter bags (Figs. 4B and 5B). Approximately 68 and 58% of the organic nitrogen remained in the root litter bags and rhizome litter bags, respectively.

THALASSIA TESTUDINUM. *Thalassia* rhizomes decayed much more slowly than *Zostera* rhizomes (Fig. 7). In one study beginning in December less than 10% of the organic matter had disappeared from the rhizomes after 247 days. *Thalassia* roots lost approximately 55% of their weight in the first 14 days and continued to lose weight slowly for the next 233 days (Fig. 7). Results of the second incu-

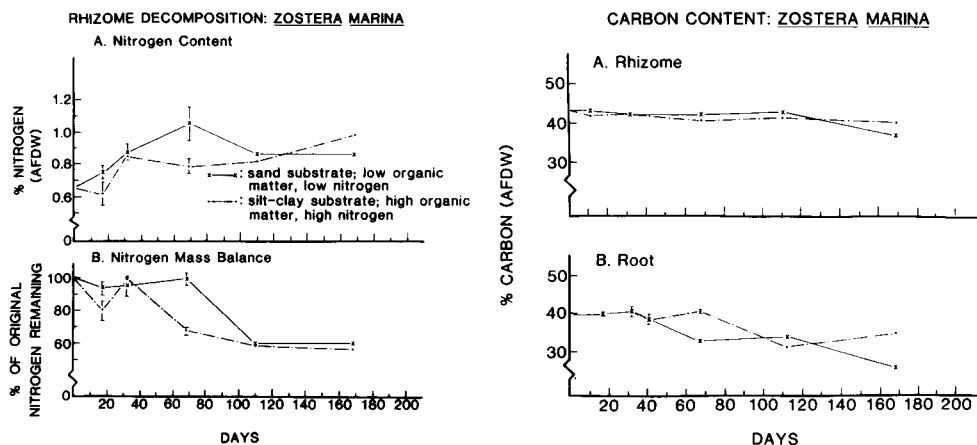


Figure 5. (Left) Changes in the nitrogen content (A) and mass of nitrogen [B] for *Zostera marina* rhizomes in litter bags buried in a seagrass bed in North Carolina between April 1981 and September 1981. See figure for legend. Bars indicate ± 1 SE.

Figure 6. (Right) Changes in the carbon content of *Zostera marina* rhizomes (A) and roots (B) in litter bags buried in a seagrass bed in North Carolina between April 1981 and September 1981. See Figure 5 for legend. Bars indicate ± 1 SE.

bation, started in May, were similar to the first 100 days of the incubation begun in December.

Over the course of 247 days, percent nitrogen of the roots and rhizomes, although fluctuating, increased slightly for roots, and decreased for rhizomes (Fig. 8). The percentage of carbon in both root and rhizome litter bags remained nearly constant throughout the incubation.

Production and Utilization of DOC.—Dried, sterilized roots and rhizomes of *Z. marina* incubated in filtered, sterilized seawater leached an average of 37.1% of

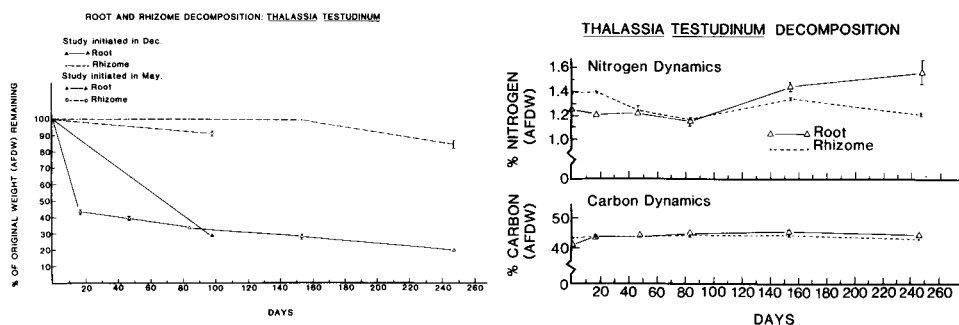


Figure 7. (Left) Weight loss (ash free dry weight) for *Thalassia testudinum* roots and rhizomes in litter bags buried in a *T. testudinum* bed in Florida Bay between December 1982 and August 1983. See figure for legend. Bars indicate ± 1 SE.

Figure 8. (Right) Changes in the nitrogen and carbon content of *Thalassia testudinum* roots and rhizomes in litter bags buried in a *T. testudinum* bed in Florida Bay between December 1982 and August 1983. See figure for legends. Bars indicate ± 1 SE.

Table 3. Summary data for calculating the amount of dissolved organic carbon (DOC) released by sterilized *Zostera marina* during a 70.5 h incubation

Source	Flask no.	Plant dry wt. (mg)	Particulate carbon in plant (mg)	Total DOC released (mg)	DOC as % of initial carbon	\bar{x} %
Leaf	2	244	89	23.3	26	27.6
Leaf	3	228	94	24.6	29.2	
Root/rhizome	4	272	78	27.4	35.1	37.1
Root/rhizome	5	239	69	23.1	39.2	

their original carbon as DOC (Table 3). The lost DOC in the roots and rhizomes (37.1%) exceeded the proportional loss of DOC by the leaves (27.6%).

Aerobic, heterotrophic bacteria from a seawater inoculum grew to cell densities of nearly 10^8 cells ml^{-1} in a treatment with DOC originating from root-rhizome leachate (Fig. 9). Bacteria utilized root-rhizome DOC as well as leaf DOC, and in both cases grew to densities an order of magnitude greater than an inoculum in unamended, filtered seawater.

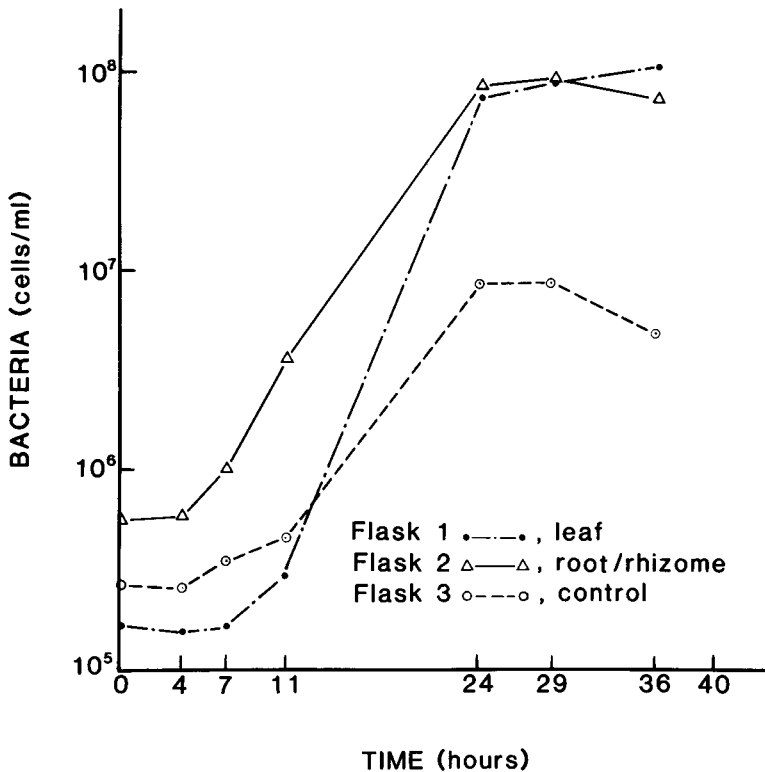


Figure 9. Growth of bacteria from a seawater inoculum in two flasks amended with the addition of a dissolved organic carbon (DOC) leached from the leaves and roots/rhizomes of *Zostera marina*, and a control flask without plant DOC.

Table 4. Sources and characteristics of organic inputs to estuarine sediments originating from primary production in an eelgrass meadow

Source of primary production	Location	Mode of incorporation into sediment	Quality	Quantity $\text{g C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$
1. Phytoplankton	Water column	External	Good/rapid turnover	50–300
2. Benthic microalgae	Sediment surface and subsurface	External/internal	Good/rapid turnover	30–200
3. Benthic macroalgae	Sediment surface	External	Moderate/intermediate turnover	50–75
4. Seagrass leaves/epiphytes	Water column	External	Resistant/slower turnover	300–400
5. Seagrass roots and rhizomes	Sediment subsurface and surface	Internal	Resistant/slower turnover	55–182
6. Plant exudates	Sediment surface and subsurface	Internal/external	Good/rapid turnover	Not quantified
7. Allocthonous	Sediment surface and subsurface	External	Variable	Not quantified

DISCUSSION

Roots and rhizomes are a substantial portion of the plant biomass in communities dominated by seagrasses (Fig. 2; Table 1). Yet leaf and epiphyte production has been emphasized in past studies (Short, 1975; McRoy and McMillan, 1977; Zieman and Wetzel, 1980), conveying a notion that the below-ground biomass may be relatively unimportant. We maintain, however, that the organic detritus originating from the roots and rhizomes is important for heterotrophic processes involved in ecosystem energetics and benthic nutrient cycles.

The absence of production data for roots and rhizomes is also a result of the lack of reliable techniques for measuring this production. Recently, however, a leaf marking technique was developed that enabled us to measure in situ below-ground production of *Zostera* (Jacobs, 1979; Kenworthy, 1981). A similar technique used for *T. testudinum* (Patriquin, 1973), has not been widely applied. Thus our most reliable estimates for below-ground organic matter production are for the temperate seagrass ecosystem dominated by *Z. marina*. The range of estimates, $55\text{--}182 \text{ g C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$, is derived from a broad geographical area extending from the southernmost distribution of eelgrass along the Atlantic coast of North America, in North Carolina, to generally more northern areas of the European coast, which are close to the geographical center of the species range (Thayer et al., in press).

We assembled the information in Table 4 to illustrate a comparison of the sources of primary production in a *Z. marina* meadow in North Carolina. For sediments, there are several sources of organic matter originating from primary production but many of the sources are unquantified or difficult to estimate (Table 4). The sources fall into categories that might be considered internal, i.e., produced on the surface or within the sediment, or external, i.e., produced within the water column before settling onto the sediment surface.

In a seagrass meadow, probably more seagrass leaves and epiphytes than phytoplankton, are incorporated into the sediments. The quantity of seagrass leaves incorporated into the sediments is likely to be quite variable and depends to some extent on specific habitat characteristics (Bach et al., unpubl. manuscript,² Wapora Inc., Atlanta, Ga.; Zieman et al., 1979). Since seagrass leaves may begin senescence even before exfoliation, they may be of different physico-chemical composition by the time they reach the sediment surface. Some seagrasses, for example *Syringodium* and *Thalassia*, float for extended periods, hence some of the leaf decay may occur in the water column (Robertson, 1982). A portion of the phytoplankton either is consumed in the water column or reaches the sediment in a different form or composition. Additionally, in shallow water all materials deposited on the sediment surface may be resuspended by waves and currents.

A physical or biological catalyst (e.g., bioturbation) is required to incorporate all external sources of organic matter into the subsurface sediments. An important aspect of root-rhizome production is that it occurs in the sediments initially. The roots and rhizomes are deposited directly into the sediment and represent the major internal source of organic matter. Since this material is usually buried it is less subject to transport processes. Unless they are uprooted by severe storms, ice rafting or bioturbation, most roots and rhizomes complete the cycle of production and decay at the site of their formation.

Benthic microalgae probably are nearest to roots and rhizomes as a direct source of organic matter to the sediment. The information for benthic microalgae is mostly derived from unvegetated sediments, and since light is attenuated by the seagrass canopy, the actual values are probably at the lower range of those presented in Table 1. Benthic macroalgae may be a large source for the sediment surface but quantitative estimates of their productivity are uncertain.

Rhizomes of both *Zostera* and *Thalassia* have a relatively larger proportion of structural material, a lower nitrogen content, and a higher C:N ratio than leaves (Table 2). These parameters also are greater than for other sources of primary production, except perhaps marsh grasses, which for this discussion we consider in the allochthonous category. We initially characterized the root-rhizome material as being resistant to decay and having a slow turnover rate. Somewhat unexpected, however, were results from the litter bag studies for *Zostera* rhizomes (Fig. 3). Loss of approximately 50–60% of the organic weight within 170 days indicates that this organic matter is a readily available source of energy and nutrients. The decay rate of *Zostera* roots and rhizomes declined toward the end of the incubation, implying that some of the organic matter is retained in the sediment from year to year, thus the pool of organic matter in the sediments consists of this detritus in varying stages of decomposition. Since *Zostera* sediments are usually anoxic (Kenworthy et al., 1982), and the lignin fractions (lignocellulose) are not known to decompose under anaerobic conditions (Hackett et al., 1977; Ziekus, 1981), some portion of the detrital roots and rhizomes probably remains in the sediment as highly recalcitrant organic residue and reacts with other organic and inorganic materials to form humic substances (Rice, 1982).

Our litter bag data suggested that during the first few weeks *Thalassia* and *Zostera* roots released a greater proportion of soluble organic matter than did the rhizomes (Figs. 3 and 7). In the first two weeks *Thalassia* roots lost approximately 55% of their weight compared to 25% for eelgrass roots. The soluble leachate from *Zostera* roots and rhizomes is a suitable substrate for micro-heterotrophic organisms. Flask incubations demonstrated that aerobic heterotrophic bacteria

² Bach, S. C., G. W. Thayer and M. W. LaCroix. Export of detritus from eelgrass (*Zostera marina*) beds near Beaufort, N.C. Unpublished.

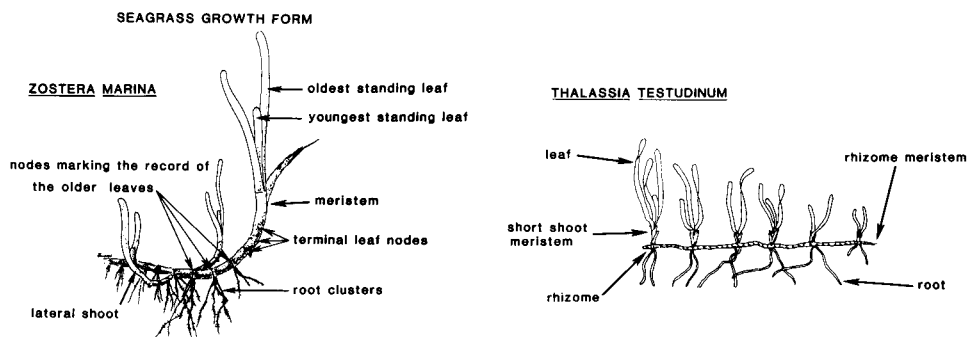


Figure 10. An illustration showing the growth form of two seagrasses, *Thalassia testudinum* and *Zostera marina*.

utilized the DOC originating from eelgrass roots and rhizomes equally as well as that originating from leaves (Fig. 9).

Decomposition of the particulate root material remaining after the initial leaching period appears to be very similar for both species. Both plants decomposed slowly, hence a substantial proportion of the root material also must be retained in the sediment organic matter pool and carried over from year to year.

The slow decay rate of *Thalassia* rhizomes suggests that even after they are physiologically disconnected from the photosynthetic organ the rhizomes retain their organic matter for long periods. The growth form and longevity of *Thalassia* short shoots also support this suggestion. *Thalassia* short shoots grow upward from a basal meristem and remain physiologically integrated with the rhizome (Fig. 10). The rhizome meristem grows through the sediment independent of the leaf meristems on the short shoots. Since adjacent short shoots may live as long as 10 years (Patriquin, 1973) the organic matter of the rhizome lives for at least that long.

In contrast, a *Zostera* shoot has a much shorter life history, usually 2 years or less, and a different arrangement between the meristem, shoot and rhizome axis. The meristem at the base of the eelgrass shoot divides by intercalary growth and the shoots grow away from the rhizome with the meristem (Fig. 10). Since the rhizome eventually becomes isolated from the photosynthetic tissue of the plant, it ceases to grow and begins senescence while still connected to the plant unit. Senescence is initiated after approximately 100–150 days. In addition, the death of 10–30% of the plant population after the annual flowering cycle, contributes a large amount of below-ground detritus each year.

Because senescence of *Zostera* rhizomes is initiated during the same year in which the rhizome forms, and because decomposition rates are faster than for *Thalassia*, we hypothesize that the nutrient cycles and pathways of energy flow in sediments of temperate eelgrass meadows involve sources, sinks and processes quantitatively distinguishable from those of tropical *Thalassia* meadows. Although biomass, and perhaps net production, of roots and rhizomes may be greater, the availability of material to the organic detritus pool in a *Thalassia* meadow probably is less than in *Zostera* meadow because the senescence and decomposition process rates are different.

We compared the decomposition rate of *Zostera* roots and rhizomes in sediments having measurably different nutrient regimes: a silt-clay sediment that had

larger quantities of organic matter, total nitrogen and dissolved and exchangeable ammonium than a relatively nutrient depleted sand substrate (Kenworthy et al., 1982) (Fig. 3). At least during the initial stages we were unable to detect any real measurable differences in the rates of decay between the sediments. The lack of any differences corroborates the hypothesis of Tenore et al. (1979; 1982) that nutrient enrichment by extrinsic sources does not necessarily stimulate the decay rate of vascular plant detritus, which initially is low in organic nitrogen but high in structural carbohydrates. Similarly Reed (1981) found that additions of inorganic nitrogen or phosphorus failed to stimulate decomposition of *Spartina alterniflora* roots in an anoxic flow through microcosm. Since *Spartina* roots, like *Zostera* and *Thalassia*, have relatively large proportions of structural material (Reed, 1981) and are low in nitrogen, we would expect to observe comparable decay processes. Reed argued that because energy transfer is less efficient under anaerobic conditions, bacteria must process more substrate. Since the bacteria must process more substrate, more nutrients associated with the particulate organic matter become available for incorporation into bacterial biomass, decreasing the need for extrinsic sources of inorganic nutrients.

During the latter part of the litter bag incubations there was some indication that decomposition may have been stimulated in the organic sediment; however, our small sample size impaired testing for differences. Possibly during a lengthy aging process, the structural nature of the detritus would be altered. Structural changes in the plant tissue increase the available sites of invasion for microorganisms. The addition of nutrients for an extended period may enhance the biomass and heterotrophic activity of microfauna and meiofauna even though the nutrients in the plant tissue are depleted during the latter stages of decay.

Invasion sites enabling microorganisms and meiofauna to colonize the interior portions of roots and rhizomes are probably very important in the decomposition of the particulate fraction, and may even be a major rate-limiting factor (Reed, 1981). Since the material is buried, it is not subjected to the abrasive action of waves, currents and moving particles. Particle size reduction, which is thought to be an important process for accelerating seagrass leaf decay (Harrison and Mann, 1975; Robertson and Mann, 1980), may be restricted to enzymatic disintegration of the cellular integrity of the roots and rhizomes by bacteria. Our observations confirm that most of the initial decay of the rhizomes occurs from within the interior portions of the material. As decomposition proceeds the interior of the rhizome becomes a void, and at a very advanced stage of decay the rhizome is an empty cylinder of organic matter. Formation of invasion sites on the surfaces of the roots and rhizomes would enable bacteria, or for that matter, any organism, to avoid the lignified walls of the periphery cells and gain access to the interior material, which is evidently less resistant to decay than the walls.

The anoxic environment and the recalcitrant nature of root and rhizome detritus probably limits the types and overall abundance of meiofauna (protozoans and ciliates) and macrofauna (burrowers and subsurface deposit feeders) that may consume or macerate the organic matter or that may act as predators on bacteria growing on the particulate organic matter. The presence of bacterial grazers is known to increase microbial biomass, stimulate microbial activity and enhance the mineralization rate of detritus (Fenchel and Harrison, 1976; Harrison, 1977; Findlay, 1981). We hypothesize that the occurrence of bacterial predators and the timing of their occurrence is one of the more important factors controlling the turnover rate of root and rhizome detritus.

There was an indication that the nitrogen content of decaying material, especially of *Zostera* roots and rhizomes, increased (Figs. 5 and 6). We did not de-

termine, however, if this increase may have occurred because of microbial or meiofaunal growth (Harrison and Mann, 1976; Tenore et al., 1982) or because of adsorption of extrinsic inorganic and organic nitrogen onto the detritus (Rice, 1982). Whatever the case, there appears to be a slow aging process in which the carbon to nitrogen ratio declines in the slowly decomposing particulate organic matter. The rate of weight loss for the particulate fraction of eelgrass roots and rhizomes, however, is sufficiently rapid to indicate that the material is not a long-term nitrogen sink (Figs. 4B and 5B).

The net production and biomass of seagrass roots and rhizomes reported in this study is much lower than for emergent wetland plants such as *Spartina* and *Juncus* (Valiela et al., 1976; Good et al., 1982). However, the functional role of the below-ground components of seagrasses in forming an important source of organic detritus in subtidal estuarine sediments should be qualitatively comparable. The soluble fraction of the material is a labile source of dissolved organic carbon for heterotrophic microorganisms. Anaerobic degradation of the particulate fraction, consisting largely of celluloses and hemicelluloses, should yield organic substrates for bacteria involved in sulfate reduction, nitrogen fixation and methanogenesis. The slow decay rate of roots and rhizomes insures that a large reservoir of decomposing organic matter is available in the sediments during periodic fluctuations in the primary production of the seagrass, benthic algae or water column. Unvegetated sediments occurring within a meadow frequently have large pools of root and rhizome detritus. Hence, secondary production of benthic organisms, which are able to derive energy and nutrients from root and rhizome detritus, may continue even in the absence of a productive seagrass canopy or water column.

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